# Crustacean assemblages of coastal wetlands from fragmented and scarcely isolated islands compared with the mainland

Lucena-Moya, Paloma

2017

Lucena-Moya , P , Gascon , S , Boix , D , Pardo , I , Sala , J & Quintana , X D 2017 , ' Crustacean assemblages of coastal wetlands from fragmented and scarcely isolated islands compared with the mainland ' , Marine and Freshwater Research , vol. 68 , no. 5 , pp. 889-899 . https://doi.org/10.1071/MF15457

http://hdl.handle.net/10138/309601
https://doi.org/10.1071/MF15457

Full citation:

Lucena-Moya, P., Gascón, S., Boix, D., Pardo, I., Sala, J., & Quintana, X. D. (2017). Crustacean assemblages of coastal wetlands from fragmented and scarcely isolated islands compared with the mainland. *Marine and Freshwater Research*, *68*(5), 889-899.

# Crustacean assemblages of coastal wetlands from fragmented and scarcely isolated islands compared with the mainland

*Paloma Lucena-Moya*[A,B,D,E], *Stéphanie Gascón*[C], *Daniel Boix*[C], *Isabel Pardo*[A], *Jordi Sala*[C] *and Xavier D. Quintana*[C]

[A]Department of Ecology and Animal Biology. University of Vigo. Campus Lagoas-Marcosende. E-36310-Vigo, Spain.

[B]Tvärminne Zoological Station, University of Helsinki. J.A. Palménin tie, 260. 10900-Hanko, Finland.

[C]GRECO, Institute of Aquatic Ecology, University of Girona. Campus de Montilivi.

E-17071-Girona, Spain.

[D]Present address: Tvärminne Zoological Station, University of Helsinki, J. A. Palménin tie, 260, 10900-Hanko, Finland.

[E]Corresponding author. Email: palomalucenamoya@gmail.com

The present study compared crustacean assemblages from coastal wetlands between a fragment archipelago and a landmass. The study included four typical crustacean taxonomic groups (i.e. Cladocera, Copepoda, Ostracoda and Malacostraca) from the Balearic Archipelago region as an example of a fragment island ('Archipelago') and the Catalonia region as the landmass ('Mainland'; Spanish Mediterranean coast). We tested null hypotheses based on the expected similarity between Archipelago and Mainland in terms of crustacean assemblages and biodiversity. Similar relationships of those community attributes with environmental variables were also expected in both regions. The results partially met the null hypotheses. We found that crustacean taxonomic composition varied between Archipelago and Mainland, likely due to peculiar biological and biogeographical processes acting in the Archipelago. The relationship between crustacean assemblages and the environmental variables was mostly similar between Archipelago and Mainland, as expected. Both regions also showed similar patterns of species distribution (i.e. Archipelago and Mainland coastal wetlands were characterised by a

few dominant species). This result could be masked by the 'filter' effect exercised by the harsh conditions of coastal wetlands. Moreover, the total diversity values (gamma biodiversity) in the Archipelago were similar to the values for the Mainland, supporting the hypothesis that fragment islands can be of substantial value for the conservation of global biodiversity.

**Additional keywords**: crustacean diversity, fragment islands, island biogeography, Mediterranean ecoregion.

## Introduction

The study of island biogeography has produced an extensive number of theories, models and tests, not only for biogeography, but also for evolution and ecology (e.g. MacArthur and Wilson 1967; Diamond 1975; Whittaker and Fernández-Palacios 2007). Different categorisations of islands, depending on the geological mechanism of their origins, are possible, for example oceanic islands, continental fragments, continental shelf islands, land-bridge islands (Darwin 1859; Wallace 1902; Whittaker and Fernández-Palacios 2007). In the present study, we followed the more generalised 'Darwinian' and 'fragment' island concepts suggested by Gillespie and Roderick (2002). Darwinian islands include those islands formed de novo, and the best known are the oceanic islands. In addition, some mangrove islands and rock pools could be included within this category (Gillespie and Roderick 2002). Fragment islands include those islands that are separated fragments from continents or mainland landmasses. The best known fragment islands are the continental islands, although we could also include isolated habitats within this category (Gillespie and Roderick 2002). In the present study, when we refer to 'Darwinian' and 'fragment' islands, we are only considering the case of oceanic and continental islands respectively.

Fragment and Darwinian islands are expected to have different roles in key ecological processes, such as immigration. For example, communities that are nearly saturated with species and have well-established biotic interactions can reduce the risk of potential colonisers (e.g. alien species; Shurin 2000; De Meester et al. 2002). In this sense, fragment islands should have a biota similar to their continental sources and the ecological niches would be filled to the point that the establishment of new species was hampered. Nevertheless, the magnitude of the effects of these ecological processes and, consequently, the expected assemblage characteristics and community structure will be ultimately determined by the isolation level of the island. Distance from the continent, the level of habitat dissimilarity and the dispersion capacity of the colonisers are main aspects to consider in establishing the scale of isolation (Gillespie and Roderick 2002). Three scales of isolation can be generally described, namely low, intermediate or high, which can be applied to both Darwinian and fragment islands (Gillespie and Roderick 2002). Evidence of the ecological processes that took place in Darwinian islands (or high-intermediate isolated fragmented islands) is widely known (e.g. Darwin 1859; Simon 1987; Gillespie et al. 2008),

whereas empirical studies in fragment islands are scarce, probably because it is less appealing to find no significant differences between island and mainland ecological dynamics, as could be expected.

Coastal wetlands are naturally stressed environments (Barnes 1989; Basset et al. 2006; Pérez-Ruzafa et al. 2011). This environmental stress is caused by the effects of variable physical factors, such as tides, storms, winds or flows (Quintana et al. 1998; Pérez-Ruzafa et al. 2005; Ciavatta and Pastres 2011), as well as the intermediate position between freshwater and marine, and between freshwater and land interfaces (Kjerfve 1994; Comín et al. 2004; Dauvin 2007). In this context, it is interesting to highlight that the Mediterranean region is characterised by a high seasonality, accompanied by sharp changes in water regimens (Alvarez Cobelas et al. 2005; Beklioglu et al. 2007). This unstable hydrological regimen has been related to strong changes in community composition and in population dynamics (e.g. Guelorget and Perthuisot 1983; Gascón et al. 2007). In the present study, we examined the crustacean assemblages of coastal wetlands from a fragmented and scarcely isolated archipelago and compared them with the crustacean assemblages of a mainland landmass. We selected the best represented groups occurring in coastal wetlands (Cladocera, Copepoda, Ostracoda and Malacostraca). In particular: (1) Cladocera, Copepoda, Ostracoda and Malacostraca are considered key groups for wetland food webs (Jeppesen et al. 2007; Brucet et al. 2010; Jensen et al. 2010); (2) they represent a high proportion of the metazoan biodiversity (Boix et al. 2007; Brucet et al. 2009); (3) some species are physiologically well adapted to these stressful environments (e.g. Kevrekidis et al. 2000; Brucet et al. 2009); and (4) some groups have a high dispersal capacity (Louette and De Meester 2005; Frisch et al. 2006) through different vectors that could act at different geographical scales (Havel and Shurin 2004), such as amphibians or wind (Vanschoenwinkel et al. 2008), birds (Green et al. 2008), fish (Beladjal et al. 2007) and even humans (Rossi et al. 2003; García-Berthou et al. 2007).

As a case study of fragment islands, we selected the Mediterranean Balearic Archipelago (Mediterranean Spain), located less than 100 km from the mainland (i.e. Catalonia). The response of crustacean assemblages to the main environmental variables was compared between the Balearic Archipelago and Catalonia. The main aim of the present study was to evaluate differences in crustacean diversity and structure between the mainland and fragment island at the species and assemblage levels, contributing to the limited literature published regarding fragment islands scarcely isolated. The main hypothesis tested was that crustacean assemblages and their responses to environmental variables are expected to be similar between the Balearic Archipelago and the mainland landmass (Catalonia; hereafter ‘Mainland’). Moreover, partial null hypotheses that supported the main hypothesis were tested, namely: (1) the environmental variables that best fit the species variability in the crustacean assemblages will not vary between

the Archipelago and Mainland; (2) different diversity values measured at different scales (α, β and γ) will not be found between the Archipelago and Mainland; and (3) the relationships between the number of crustacean species and the environmental variables will not vary between the Archipelago and Mainland.

## Material and methods

### *Areas of study*

The study was performed in coastal wetlands from two Spanish Mediterranean regions: Catalonia (north-eastern Iberian Peninsula; Mainland) and the Balearic Archipelago (Western Mediterranean sea; 'Archipelago') located ~100 km from the Spanish east coast (Fig. 1). Coastal wetlands from the four principal islands of this Archipelago (i.e. Majorca, Minorca, Ibiza and Formentera) were sampled in the present study. Both the Mainland and the Archipelago sites belong to the Mediterranean ecoregion, characterised by dry summers and mild winters, with rainfall occurring mainly during autumn and spring (Britton and Crivelli 1993). All coastal wetlands studied were permanent and brackish. Although the Mediterranean Sea has a microtidal range (<2 m; Davies 1964), all the coastal wetlands studied were marine influenced and shallow (maximum depth <6 m).

### *Sampling procedure*

Mainland data were obtained from surveys conducted at 32 coastal wetlands (one sampling site per wetland, yielding 32 sites). In the Archipelago, surveys were conducted at 23 coastal wetlands. In three of the wetlands, more than one sampling site was established due to the size and within-habitat heterogeneity, yielding 32 sampling sites. The study was performed during winter (February–March) and spring (May–June) in 1996, 1997, 2000, 2003 (Mainland) and 2006 (Archipelago) to reflect temporal variability.

Water temperature, electrical conductivity, percentage oxygen saturation and pH were measured *in situ*, whereas dissolved inorganic nutrients (ammonium, nitrite, nitrate and phosphate) and chlorophyll-*a* (Chl-*a*) content were analysed in the laboratory. Details of the analytical protocols for these variables can be found in Boix et al. (2008) for the Mainland sites and Lucena-Moya et al. (2009) for the Archipelago sites. The coastal wetland surface area (size) was calculated using freely available aerial photographs (Departament de Política Territorial i Obres Públiques 2005; Ministerio de Agricultura Pesca y Alimentación 2006). Additional information on the characterisation of the coastal wetlands (chemistry of the water and size) is summarised in Table 1.

Crustacean samples were collected accounting for the possible different microhabitats within each sampling site (e.g. shores with and without vegetation, submerged vegetation, bare sediment). Thus, a sampling effort proportional to the representativeness of each microhabitat

was performed at each site. A hand net with a mesh size of 250 μm was used. A fixed number of 'sweeps' (10 and 20 in the Archipelago and Mainland respectively) was undertaken at each sampling site. The abundance data were calculated as catch per unit effort (CPUE; i.e. individuals per sweep). Each 'sweep' consisted of a rapid push through the water column and on the bottom.

*Data analysis*

*Environmental characterisation*

To test the significance of differences in the environmental characterisation of the coastal wetlands over space and time, comparisons were made between the following groups: Group 1, Mainland-winter; Group 2, Mainland-spring; Group 3, Archipelago-winter; Group 4, Archipelago-spring. A multivariate approach based on principal components analysis (PCA) coupled with between-group analyses was used (Dolédec and Chessel 1989). The between-group analysis allowed us to obtain the centroid of each group. Differences among groups were checked using a Monte Carlo permutation test (999 unrestricted permutations under a reduced model). The PCA was performed by applying the function 'duddi.pca', centroids were calculated by means of the function 'between' and a Monte Carlo test was performed using the function 'randtest.between'. These three functions can be found in the ade4 library written in the R language (R Foundation for Statistical Computing, Vienna, Austria) (Dray and Dufour 2007). Variables were log transformed ($\log(x + 1)$) when necessary and standardised (by the maximum). The dataset analysed contained a total of 128 data samples (32 sites × 2 seasons = 64 samples for each region of study) and eight environmental variables (water temperature, electrical conductivity, percentage oxygen saturation, pH, dissolved inorganic nitrogen (DIN; obtained by summing nitrogen fractions: ammonium + nitrite + nitrate), phosphate, Chl-*a* and water body size).

*Composition of crustacean assemblages and environmental variables*

Similarity percentage analysis (SIMPER) was used to detect characteristic crustacean species on coastal wetlands. This analysis examines the contribution of individual species to the average dissimilarity between pairs of groups (Archipelago *v*. Mainland) and resemblances within a group (Archipelago and Mainland) using Bray–Curtis similarities. Absence and presence data per site were used and the region of study (Archipelago *v.* Mainland) was included as a factor. The SIMPER analysis was performed using PRIMER 6 (PRIMER-E Ltd.) (Clarke and Warwick 2001).

Canonical correspondence analyses (CCAs) were performed to identify the environmental variables that best fit the species variability in the crustacean assemblages. A combined CCA (i.e. Mainland and Archipelago together) was first performed to quantify the regional effect

through their conditional effect. Another two CCAs were performed for each separate region (i.e. one for Mainland and another for Archipelago) to identify whether the environmental variables related to the crustacean assemblages were similar across regions. All the species abundance matrices used (93 taxa for Archipelago and Mainland combined; 66 taxa for Mainland; 58 taxa for Archipelago) were square root transformed. We downweighted for rare species to reduce their influence in the analysis (ter Braak and Šmilauer 1998). All environmental variables ($n$ = 8) were log transformed (log($x$ + 1)), except pH and region. Season (spring and winter) was taken into account as a covariate. The forward selection procedure was used to obtain the conditional effect (λ) for each variable, and expressed as a percentage. Two significance tests for canonical axes were performed using the Monte Carlo test (499 permutations). The first test shows whether the first canonical axis is sufficient to explain species variation. The second permutation test (with all canonical axes) verifies the existence of a relationship between environmental parameters and species matrix. CCAs were performed using CANOCO 4.5 (ter Braak and Šmilauer 1998).

*Crustacean diversity and environmental variables*

We used three approaches to analyse values of diversity in the Archipelago and Mainland for each taxonomic group of crustaceans (Cladocera, Copepoda, Ostracoda and Malacostraca), as detailed below.

1. α Diversity as mean species richness per site. Significant differences in α diversity values between the Mainland and Archipelago were tested for each crustacean taxonomic group using either Kruskal–Wallis H test or one-way analysis of variance (ANOVA) tests depending on whether the parametric assumptions were met.

2. β Diversity as multiple-site similarity measures independent of patterns of richness (Baselga et al. 2007; Baselga 2010). Because β diversity may be caused by two different phenomena, namely nestedness (reflecting a process of species loss) and species turnover (implying the replacement of some species by others; Harrison et al. 1992; Baselga et al. 2007; Baselga 2010), we assessed the overall multiple-site dissimilarities, considering total β diversity (Sørensen-based multiple-site dissimilarity; βSOR), spatial turnover (Simpson-based multiple-site dissimilarity; βSIM) and nestedness (nestedness-resultant multiple-site dissimilarity (βNES), which is inferred: βNES = βSOR – βSIM) components. Calculations were performed using the free software R (R Foundation for Statistical Computing, Vienna, Austria) and followed functions and scripts described in Baselga et al. (2007) and Baselga (2010).

3. γ Diversity as the total richness for each region, calculated using the Chao2 estimator (EstimateS: statistical estimation of species richness and shared species from samples,

version 8.2; http://viceroy.eeb.uconn.edu/estimates/, accessed 15 January 2015). This estimator is a highly recommended measure of total richness because it is independent of possible differences in the sampling effort (Magurran 2013). The bias-corrected formula of the Chao2 estimator was used when Chao's estimated CV for abundance distribution was <0.5; otherwise, a classic Chao2 estimator was used To determine whether the results obtained with the Chao2 estimator were significantly different ($P < 0.05$), the criterion used was the absence of overlap among the 95% confidence intervals (CIs) of the coastal wetlands (Colwell et al. 2004).

The relationships between species richness and the environmental variables were explored by means of linear mixed effects (LME) models. The categorical spatial variable region (i.e. Archipelago or Mainland) was introduced as a dummy variable. The model was mixed because the explanatory variables are a mixture of fixed (regions of study) and random (season: winter and spring) factors. Residual plots were checked for model assumptions. We started with the most complex model taking into account the double interactions with the 'region' factor. The residual maximum likelihood (REML) method was used to find the fittest and most parsimonious model (see Venables and Ripley 2002). All models were estimated by the LME function in the lme library written in the R language (Pinheiro and Bates 2000).

## Results

*Environmental characterisation*

A comparison of centroids from the PCA ordination showed no significant differences between Mainland-winter and Archipelago-winter groups ($P > 0.05$) or between Mainland-spring and Archipelago-spring groups ($P > 0.05$) in the environmental characterisation of the coastal wetlands (Fig. 2; Table 1). However, significant differences were found between seasons within the same region (e.g. Archipelago-winter *v.* Archipelago-spring), reinforcing the importance of seasonality in Mediterranean areas.

*Composition of crustacean assemblages and environmental variables*

In all, 93 crustacean species were recorded in the Archipelago ($n = 58$) and Mainland ($n = 67$) systems (see Table S1, available as Supplementary Material to this paper). Furthermore, 27 crustacean species were found exclusively in the Archipelago, whereas 35 were found in the Mainland (Table S1). Ostracods and copepods had the highest occurrence among all the crustaceans; specifically, copepods were present in every sample from the Mainland (Table 2). Malacostracans showed a high occurrence, but only in the Archipelago, and cladocerans had the lowest occurrence in both regions (Table 2). The percentage of common species was always higher (Cladocera and Copepoda) or slightly higher (Ostracoda) in the Archipelago than in the Mainland, except for Malacostraca (Table 2).

SIMPER analysis showed a high dissimilarity (>80%) between the regions (Archipelago *v*. Mainland) for the crustacean composition (Table 3). Furthermore, a low similarity within Mainland (~20%) and Archipelago (~25%) should be noted because it indicates a high variability within regions. Taxa that best characterised the crustacean assemblages of the Archipelago were the ostracod *Cyprideis torosa* (25.91%) and the two malacostracans *Gammarus aequicauda* and *Lekanesphaera hookeri* (22.14% and 19.63% respectively; Table 3). The crustacean assemblages of the Mainland were characterised by the copepod *Acanthocyclops* gr. *robustus* (32.99%) and the malacostracan *Gammarus aequicauda* (25.55%). Moreover, the Mainland included characteristic crustacean species missing from the Archipelago (two copepods (*Diacyclops bicuspidatus* and *Eurytemora velox*), one ostracod (*Cypridopsis vidua*) and one cladoceran (*Daphnia pulicaria*); Table 3).

In relation to the explanatory variables that best fit the species variability in the crustacean assemblages, the factor 'region' explained the highest percentage (24.66%) of the crustacean variability for the combined CCA (i.e. Archipelago and Mainland together; Table 4). Conversely, analysis for each region separately (i.e. Archipelago CCA and Mainland CCA) showed that ~50% of the variability in the crustacean assemblages was explained by the same variables in both regions (i.e. electric conductivity, size and DIN; Table 4).

*Crustacean diversity and environmental variables*

Significant differences were observed for the α diversity. Specifically, the mean richness of Cladocera and Copepoda was significantly higher in the Mainland than in the Archipelago ($H$ = 5.98 (d.f. = 1, $P$ = 0.0145) and $H$ = 44.98 (d.f. = 1, $P < 0.001$) respectively; Fig. 3a). Conversely, the mean richness of Malacostraca and Ostracoda was significantly higher in the Archipelago than in the Mainland ($F_{1,126}$ = 10.6 ($P$ = 0.001) and $H$ = 8.67 (d.f. = 1, $P$ = 0.0032) respectively; Fig. 3a). β Diversity did not differ between the Archipelago and Mainland for all groups of crustaceans (Fig. 3b). It was observed that β diversity was due to the replacement of species ($\beta_{SIM}$) rather than species loss ($\beta_{NES}$) in both regions. Regarding γ diversity, there was no significant difference in the total estimated species richness between the Archipelago and the Mainland (Fig. 3c).

The relationships between crustacean species richness and environmental variables were not significantly different between regions, except for Malacostraca and Cladocera, for which the interaction with the factor 'region' was significant (Fig. 4; Tables S2, S3). The relationship between Malacostraca richness and electrical conductivity was positive in both regions, albeit almost ninefold stronger in the Archipelago than in the Mainland sites (Fig. 4a). There was a significant positive relationship between nutrient content (phosphate and DIN) and Malacostraca richness in the Archipelago, whereas in the Mainland this trend was reversed (Fig.

4b, c). The relationship between Cladocera richness and DIN was region dependent, but the trend was similar in both regions (i.e. negative, although markedly stronger in the Archipelago than in the Mainland; Fig. 4d).

**Discussion**

Recognising the characteristic features of different islands types (e.g. Darwinian *v.* fragment islands, according to Gillespie and Roderick 2002) is important for understanding emerging patterns, in particular speciation, biodiversity and conservation (Whittaker and Fernández-Palacios 2007; Watson 2009). Although studies on Darwinian islands are widely reported in the literature (Sauer 1969; Cowie and Holland 2006; Whittaker et al. 2008; Caujapé-Castells et al. 2010), fragment islands have received less attention. This may be related to the anticipated similarity expected between fragment islands and the mainland landmass from where they originate, being less appealing for the researchers to investigate. Because we found significant differences in the species composition of the crustacean assemblages, we are not able to confirm the null hypothesis that assumed the similarity of the crustacean assemblages between the Archipelago (Balearic Islands) and Mainland (Iberian Peninsula). Such a difference was supported by the results of the combined CCA, which determined the regional effect as the best predictor of species variability. Considering the type of variables and analyses performed in the present study, we did not have enough information to single out the causes of these differences. Nevertheless, we can think of two possible causes, the first being the effect of stochastic ecological drift and evolutionary processes at local (e.g. community level) or regional (e.g. meta-community level) scales (Hubbell 2001). The current isolation of the Archipelago began at the end of the Messinian salinity crisis, 5.3 Myr ago (Clauzon et al. 1996; Krijgsman et al. 1999), although the Archipelago suffered another regrouping during the Quaternary glaciations (Melendez-Hevia 2004). This is a sufficient time gap, biologically and geologically, so that the composition of the crustacean assemblages could differ from their source because of those processes related to the evolution and ecological drift (Lomolino et al. 2010). The second possible cause is the proximity of the coastal wetlands from the Archipelago to several land masses other than the Mainland site (e.g. by recruitment or dispersion; Barnes 1995). For example, in the present study, the Archipelago crustacean assemblage had 27 species that were not shared with the Mainland. This number of ‘exclusive species’ could be attributed to the potential influences of other regions and mainland landmasses. In fact, crustacean fauna of African origin have been found in temporary ponds in the Balearic Islands (Jaume 1989; Zamora et al. 2005).

Beyond the regional effect, most of the variability of crustacean assemblages in both regions was explained by the same environmental variables, including electrical conductivity, size and DIN. These results support other studies that found that these three variables were related to the

turnover rate of the water body (Guelorget and Perthuisot 1983; De Kroon et al. 1985). In particular, wetland size and electrical conductivity have been identified as the main drivers of the fauna in coastal wetlands throughout the world (Joyce et al. 2005; Nielsen et al. 2007) and especially the Mediterranean area (Quintana et al. 1998; Anton-Pardo and Armengol 2012). Therefore, despite the dissimilarity in the composition of the crustacean assemblages between the Archipelago and the Mainland, we can assert that their responses to environmental variables were comparable.

A marked dissimilarity in crustacean assemblages (~80%) between the Archipelago and Mainland was observed. Furthermore, a high dissimilarity was detected within regions, which reflects the variability among coastal wetlands within the Archipelago and Mainland. These results are in accordance with studies conducted in transitional waters of the Mediterranean and Black seas (Barbone and Basset 2010). These authors found that there was a patchy distribution of macroinvertebrate taxa and a low average similarity in taxa composition (~10%) among lagoons within the same region. We observed a similar pattern in both the Archipelago and Mainland consisting of the dominance of the assemblages by very few species: three species dominated in the Archipelago (*Cyprideis torosa*, *Gammarus aequicauda* and *Lekanesphaera hookeri*) and two species dominated in the Mainland (*Acanthocyclops* gr. *robustus* and *Gammarus aequicauda*). This pattern is typically expected in highly restrictive or 'filtered' environments. Thus, harsh conditions can act as a 'filter' for the community structure, causing the reduction of the community to a few species (Poff 1997; Strange and Foin 1999). Similar conclusions have been made for other Mediterranean coastal ecosystems (e.g. Barbone et al. 2007; Barbone and Basset 2010). Certainly, the Mediterranean coastal wetlands can be considered highly 'filtered' ecosystems, where the 'filter' is partly imposed by harsh and changeable environmental conditions (e.g. abrupt changes between seasons, variations in water level and salinity) and variable physical factors (e.g. storms, wind, flows) of this ecoregion (Statzner et al. 2001; Elliott and Quintino 2007). Therefore, regardless of the mainland or fragment island region, a similar pattern of crustacean community structure was observed, in accordance with our null hypothesis.

The instability and harshness of the environmental conditions of coastal wetlands can also constrain crustacean diversity in both the Mainland and Archipelago. The second proposed partial null hypothesis of equal diversity between regions was applicable to $\beta$ and $\gamma$ diversity. The comparable values of the among-systems (i.e. $\beta$) and total (i.e. $\gamma$) diversity between the Archipelago and the Mainland can be explained by a high temporal or spatial (among wetlands) turnover of species (Chalcraft et al. 2004; Anderson et al. 2011). This is supported by the high taxa occurrence, elevated dissimilarity within the wetlands and high rate of replacement of the crustacean species observed in both regions. However, within the equilibrium theory of island

biogeography, it would be expected that the turnover rate would be lower in the islands than on the continent (MacArthur and Wilson 1967; Walter 2004). However, our results support the hypothesis of similarity between fragment islands and mainland. The crustacean assemblage of the Archipelago can be supplied by the migration or colonisation from mainland landmasses, as well as migration among islands, favouring the maintenance of levels of diversity. Conversely, the Balearic Archipelago is old enough to have probably reached a fairly stable total biodiversity level. However, this scenario is different from what is happening on a smaller scale, because the α diversity values differed significantly between regions. It is expected that in fragment islands, over time and with isolation, the number of species (α diversity) on islands created by fragmentation will, if anything, decline (Gillespie and Roderick 2002). Based on this premise, it could be expected that the Mainland, being the principal source, would exhibit higher α diversity values than the Archipelago. However, this expectation was not always met, because the α diversity values were higher in the Archipelago for two taxonomic groups (Malacostraca and Ostracoda). As argued previously for the crustacean assemblage, various causes could be responsible for differences in the diversity values for those crustacean groups between regions, including environmental conditions, biological processes and biogeographical events. Furthermore, we considered crustaceans with a high component of microcrustaceans (cladocerans, ostracods, copepods), characterised by small body size, high fecundity and large geographic ranges. In previous studies, crustacean species meeting these traits were less prone to extinction following fragmentation (e.g. Cardillo 2003; Cooper et al. 2008), which could contribute to the maintenance of high levels of α diversity also in the islands. Although, we are not able to confirm the specific causes of the differences in biodiversity between the Archipelago and Mainland, it is of note that fragment and scarcely isolated islands may hold similar or even higher values of local diversity than the Mainland.

Finally, the third proposed null hypothesis regarding the relationships between environmental variables and species richness was partially met. Thus, the relationships were similar across regions, although not for all cases (i.e. Malacostraca and Cladocera responded differently to environmental variables). The similar environmental relationships observed in the present study for copepods, cladocerans and ostracods have also been found in other studies, such as a reduction of copepod diversity with an increase in water temperature (e.g. Frisch and Green 2007), decrease in diversity (cladocerans, copepods) with salinity (Boix et al. 2008; Brucet et al. 2009) and an increase of ostracod diversity with Chl-a (Allen and Dodson 2011). Malacostraca and Cladocera showed different patterns between the two regions. Different factors could be responsible for those differences. For example, a higher eutrophication range (nutrients and Chl-*a*) in the Mainland and a higher sea connectivity of the coastal wetlands in the Archipelago may favour the α diversity of typical littoral taxa such as malacostracans, as well as their positive

relationships with nutrients and electrical conductivity in the Archipelago. This is a hypothesis that needs to be tested experimentally. However, high eutrophication and sea connectivity would not be favourable environmental conditions for typical freshwater crustaceans, such as cladocerans, in the Archipelago.

## Conclusion

The Balearic Archipelago, as an example of fragment islands, met some of the proposed null hypotheses based on the expected similarity to the Mainland. These results are consistent with the fact that fragment islands are half-way between the mainland and oceanic islands (which are expected to be the most dissimilar to the mainland) and so they have characteristics of both (Novosolov and Meiri 2013). However, it is remarkable that despite the short geographic distance that separates the Balearic Archipelago from the closest mainland, these islands are the most isolated islands in the Mediterranean (Bover et al. 2008). Indeed, the Balearic Islands have been described by some as 'oceanic-like islands' (Alcover *et al*. 1998) because of their isolation and their ancient fragmentation from the mainland. Although our data showed significant differences in species richness and assemblage structure between the Archipelago and Mainland, similar environmental patterns could be identified regardless of the regional effect. Thus, we should consider that the similarity between the fragment island and mainland may be somehow cofounded by the effect of a 'filter' exerted by the ecosystem itself (i.e. coastal wetlands). The fact that fragment islands can support a diverse crustacean fauna comparable to the mainland, or even higher in some cases, provides evidence that islands in general contribute a more significant portion of global biodiversity than is commonly recognised (Walter 2004). Therefore, fragment islands are ecosystems of substantial conservation interest, although they have been less ecologically considered than oceanic islands. Fragment islands, with stable population dynamics, can be considered important faunal reservoirs that can feed back to their original sources.

## Supplementary material

Supplementary material includes a species list identified in the present study for Archipelago and Mainland (absence and presence) and two tables containing a summary of the LME results that supports Figure 4. The Supplementary material is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MF15457_AC.pdf).

## Acknowledgements

The authors thank C. Delgado, M. Domínguez, L. García, A. Nebra, M. Penalta, M. Martinoy and J. Gifre for field assistance and laboratory work, and Anna Sullivan, Charlotte Angove and Iván F. Rodil for their valuable comments and corrections of English language expression. This research was supported by the Government of the Balearic Islands (Dirección General de Recursos Hídricos), through the project

entitled ‘Implementation of the Water Framework Directive in the Balearic Islands: Evaluation of the Environmental Quality of the Surface Waters Using Biological Indicators’, the University of Vigo (P.P. 0022 122P 6480201), and by a grant from the Spanish Ministerio de Ciencia e Innovación (CGL2011-23907).

## References

Alcover, J. A., Sans, A., and Palmer, M. (1998). The extent of extinctions of mammals on islands. *Journal of Biogeography* **25**, 913–918. doi:10.1046/J.1365-2699.1998.00246.X

Alvarez Cobelas, M., Rojo, C., and Angeler, D. G. (2005). Mediterranean limnology: current status, gaps and the future. *Journal of Limnology* **64**, 13–29. doi:10.4081/JLIMNOL.2005.13

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone,A. L., Sanders,N. J.,Cornell,H.V.,Comita, L. S.,Davies,K. F., and Harrison, S. P. (2011). Navigating the multiple meanings of b diversity: a roadmap for the practicing ecologist. *Ecology Letters* **14**, 19–28. doi:10.1111/J.1461-0248.2010.01552.X

Anton-Pardo, M., and Armengol, X. (2012). Effects of salinity and water temporality on zooplankton community in coastal Mediterranean ponds. *Estuarine, Coastal and Shelf Science* **114**, 93–99. doi:10.1016/J.ECSS. 2011.08.018

Barbone, E., and Basset, A. (2010). Hydrological constraints to macrobenthic fauna biodiversity in transitional waters ecosystems. *Rendiconti Lincei* **21**, 301–314. doi:10.1007/S12210-010-0090-4

Barbone, E., Rosati, I., Pinna, M., and Basset, A. (2007). Taxonomic and dimensional structure of benthic macroinvertebrate guilds in the Margherita di Savoia Salt Pans (Italy). *Transitional Waters Bulletin* **4**, 21–31.

Barnes, R. S. K. (1989). The coastal lagoons of Britain: an overview and conservation appraisal. *Biological Conservation* **49**, 295–313. doi:10.1016/0006-3207(89)90049-9

Barnes, R. S. K. (1995). European coastal lagoons: macrotidal versus microtidal contrasts. *Biologia Marina Mediterranea* **2**, 3–7.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143. doi:10.1111/J.1466-8238.2009.00490.X

Baselga, A., Jiménez-Valverde, A., and Niccolini, G. (2007).Amultiple-site similarity measure independent of richness. *Biology Letters* **3**, 642–645. doi:10.1098/RSBL.2007.0449

Basset, A., Sabetta, L., Fonnesua, A., Mouillot, D., do Chi, T., Viaroli, P., Giordani, G., Reizopoulou, S., Abbiati, M., and Carrada, G. C. (2006). Viewpoint: typology in Mediterranean transitional waters: new challenges and perspectives. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**, 441–455. doi:10.1002/AQC.767

Beklioglu, M., Romo, S., Kagalou, I., Quintana, X. D., and Be´cares, E. (2007). State of the art in the functioning of shallow Mediterranean lakes: workshop conclusions. *Hydrobiologia* **584**, 317–326. doi:10.1007/S10750-007-0577-X

Beladjal, L., Kristof, D., and Mertens, J. (2007). Dispersal of fairy shrimp *Chirocephalus diaphanus* (Branchiopoda: Anostraca) by the trout (*Salmo trutta*). *Journal of Crustacean Biology* **27**, 71–73. doi:10.1651/S-2718.1

Boix, D., Sala, J., Gascón, S., Martinoy, M., Gifre, J., Brucet, S., Badosa, A., Lopez-Flores, R., and Quintana, X. D. (2007). Comparative biodiversity of crustaceans and aquatic insects from various water body types in coastal Mediterranean wetlands. *Hydrobiologia* **584**, 347–359. doi:10.1007/S10750-007-0579-8

Boix, D., Gasco´n, S., Sala, J., Badosa, A., Brucet, S., Lo´pez-Flores, R., Martinoy, M., Gifre, J., and Quintana, X. D. (2008). Patterns of composition and species richness of crustaceans and aquatic insects along environmental gradients in Mediterranean water bodies. *Hydrobiologia* **597**, 53–69. doi:10.1007/S10750-007-9221-Z

Bover, P., Quintana, J., and Alcover, J. A. (2008). Three islands, three worlds: paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quaternary International* **182**, 135–144. doi:10.1016/J.QUAINT.2007.06.039

Britton, R. H., and Crivelli, A. J. (1993). Wetlands of southern Europe and North Africa: Mediterranean wetlands. In 'Wetlands of the World I: Inventory, Ecology and Management'. (Eds D. F. Whigham, D. Dykyjova and S. Hejny.) pp. 129–194. (Kluwer, Academic Publishers: Dordrecht.)

Brucet, S., Boix, D., Gasco´n, S., Sala, J., Quintana, X. D., Badosa, A., Søndergaard, M., Lauridsen, T. L., and Jeppesen, E. (2009). Species richness of crustacean zooplankton and trophic structure of brackish lagoons in contrasting climate zones: north temperate Denmark and Mediterranean Catalonia (Spain). *Ecography* **32**, 692–702. doi:10.1111/J.1600-0587.2009.05823.X

Brucet, S., Boix, D., Quintana, X. D., Jensen, E., Nathansen, L. W., Trochine, C., Meerhoff, M., Gasco´n, S., and Jeppesen, E. (2010). Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: Implications for effects of climate change. *Limnology and Oceanography* **55**, 1697–1711. doi:10.4319/LO.2010.55.4.1697

Cardillo, M. (2003). Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation* **6**, 63–69. doi:10.1017/S1367943003003093

Caujape´-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F. V., Moura, M., Jardim, R., and Go´mes, I. (2010). Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 107–129. doi:10.1016/J.PPEES.2009.10.001

Chalcraft, D. R., Williams, J. W., Smith, M., and Willig, M. R. (2004). Scale dependence in the species-richness–productivity relationship: the role of species turnover. *Ecology* **85**, 2701–2708. doi:10.1890/03-0561

Ciavatta, S., and Pastres, R. (2011). Exploring the long-term and interannual variability of biogeochemical variables in coastal areas by means of a data assimilation approach. *Estuarine, Coastal and Shelf Science* **91**, 411–422. doi:10.1016/J.ECSS.2010.11.006

Clarke, K. R., and Warwick, R. M. (2001). Species analysis. In ‘Change in Marine Communities: an approach to statistical analysis and interpretation’, 2nd edn. pp. 7-1–7-4. (PRIMER-E: Plymouth, UK.)

Cauzon, G., Suc, J.-P., Gautier, F., Berger, A., and Loutre, M.-F. (1996). Alternate interpretation of the Messinian salinity crisis: controversy resolved? *Geology* **24**, 363–366. doi:10.1130/0091-7613(1996)024,0363:AIOTMS.2.3.CO;2

Colwell, R. K., Mao, C. X., and Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**, 2717–2727. doi:10.1890/03-0557

Comin, F. A., Menendez, M., and Herrera, J. A. (2004). Spatial and temporal scales for monitoring coastal aquatic ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14**, S5–S17. doi:10.1002/AQC.646

Cooper, N., Bielby, J., Thomas, G. H., and Purvis, A. (2008). Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* **17**, 211–221. doi:10.1111/J.1466-8238.2007.00355.X

Cowie, R. H., and Holland, B. S. (2006). Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography* **33**, 193–198. doi:10.1111/J.1365-2699.2005.01383.X

Darwin, C. (1859). ‘On the Origins of Species by Means of Natural Selection.’ (Murray: London.)

Dauvin, J. C. (2007). Paradox of estuarine quality: benthic indicators and indices in estuarine environments, consensus or debate for the future. *Marine Pollution Bulletin* **55**, 271–281. doi:10.1016/J.MARPOLBUL.2006.08.017

Davies, J. H. L. (1964). A morphogenic approach to world shorelines. *Zeitschrift fu¨r Geomorphologie* **8**, 127–142.

de Kroon, H., de Jong, H., and de Verhoeven, J. T. A. (1985). The macrofauna distribution in brackish inland waters in relation to chlorinity and other factors. *Hydrobiologia* **127**, 265–275. doi:10.1007/BF00024231

De Meester, L., Go´mez, A., Okamura, B., and Schwenk, K. (2002). The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecologica* **23**, 121–135 doi:10.1016/S1146-609X(02)01145-1

Departament de Polı´tica Territorial i Obres Pu´bliques (2005). Hipermapa.Atles electro`nic de Catalunya. Available at http://hipermapa.ptop.gencat.cat/hipermapa/client/151208/base_high_cat.html [Verified 8 January 2015].

Diamond, J. M. (1975). The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**, 129–146. doi:10.1016/0006-3207(75)90052-X

Dole´dec, S., and Chessel, D. (1989). Seasonal successions and spatial variables in fresh-water environments 2. Distinction between seasonal and environmental-effects within floral and faunistical data. *Acta Oecologica Oecologia Generalis* **10**, 207–232.

Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* **22**, 1–20. doi:10.18637/JSS.V022.I04

Elliott, M., and Quintino, V. (2007). The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* **54**, 640–645. doi:10.1016/J.MARPOLBUL.2007.02.003

Frisch, D., and Green, A. J. (2007). Copepods come in first: rapid colonization of new temporary ponds. *Archiv fu¨r Hydrobiologie* **168**, 289–297. doi:10.1127/1863-9135/2007/0168-0289

Frisch, D., Rodriguez-Perez, H., and Green, A. J. (2006). Invasion of artificial ponds in Don˜ana Natural Park, southwest Spain, by an exotic estuarine copepod. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**, 483–492. doi:10.1002/AQC.718

Garcı´a-Berthou, E., Boix, D., and Clavero, M. (2007). Non-indigenous animal species naturalized in Iberian inland waters. In 'Biological Invaders in Inland Waters: Profiles, Distribution, and Threats'. (Ed. F. Gherardi.) pp. 123–140. (Springer Science & Business Media.)

Gasco´n, S., Brucet, S., Sala, J., Boix, D., and Quintana, X. D. (2007). Comparison of the effects of hydrological disturbance events on benthos and plankton salt marsh communities. *Estuarine, Coastal and Shelf Science* **74**, 419–428. doi:10.1016/J.ECSS.2007.04.031 Gillespie, R. G., and Roderick, G. K. (2002). Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* **47**, 595–632. doi:10.1146/ANNUREV.ENTO.47.091201.145244

Gillespie, R. G., Claridge, E. M., and Goodacre, S. L. (2008). Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagos. *Philosophical Transactions of the Royal Society of London – B. Biological Sciences* **363**, 3335–3346. doi:10.1098/RSTB.2008.0124

Green, A. J., Jenkins, K. M., Bell, D., Morris, P. J., and Kingsford, R. T. (2008). The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology* **53**, 380–392.

Guelorget, O., and Perthuisot, J. P. (1983). 'Travaux du Laboratoire de Ge´ologie 16.' (Presse de l'Ecole Normale Supe´rieure: Paris.)

Harrison, S., Ross, S. J., and Lawton, J. H. (1992). Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61**, 151–158. doi:10.2307/5518

Havel, J. E., and Shurin, J. B. (2004). Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography* **49**, 1229–1238 doi:10.4319/LO.2004.49.4_PART_2.1229

Hubbell, S. P. (2001). 'The Unified Neutral Theory of Biodiversity and Biogeography.' (Princeton University Press: Princeton, NJ, USA.)

Jaume, D. (1989). *Metadiaptomus chevreuxi* (Copepoda: Calanoida: Diaptomidae) and *Leptestheria mayeti* (Branchiopoda: Conchostraca: Leptestheriidae), two African freshwater crustaceans recorded in Majorca. *Limnetica* **5**, 101–109.

Jensen, E., Brucet, S., Meerhoff, M., Nathansen, L., and Jeppesen, E. (2010). Community structure and diel migration of zooplankton in shallow brackish lakes: role of salinity and predators. *Hydrobiologia* **646**, 215–229. doi:10.1007/S10750-010-0172-4

Jeppesen, E., Søndergaard, M., Pedersen, A. R., Ju¨rgens, K., Strzelczak, A., Lauridsen, T. L., and Johansson, L. S. (2007). Salinity induced regime shift in shallow brackish lagoons. *Ecosystems* **10**, 48–58. doi:10.1007/S10021-006-9007-6

Joyce, C. B., Vina-Herbon, C., and Metcalfe, D. J. (2005). Biotic variation in coastal water bodies in Sussex, England: implications for saline lagoons. *Estuarine, Coastal and Shelf Science* **65**, 633–644. doi:10.1016/J.ECSS.2005.07.006

Kevrekidis, T., Mogias, A., and Gouvis, N. (2000). Interannual changes in the composition of the macrobenthic fauna of Drana lagoon (Evros Delta, N. Aegean Sea): preliminary note. *Belgian Journal of Zoology* **130**, 101–107.

Kjerfve, B. (1994). 'Coastal Lagoon Processes.' (Elsevier Science Publishers: Amsterdam.)

Krijgsman, W., Hilgen, F. J., Raffi, I., Sierro, F. J., and Wilson, D. S. (1999). Chronology, causes and progression of the Messinian salinity crisis. *Nature* **400**, 652–655. doi:10.1038/23231

Lomolino, M. V., Brown, J. H., and Sax, D. F. (2010). Island biogeography theory reticulations and reintegration of 'a biogeography of the species'. In 'Island Biogeography Theory. The Theory of Island Biogeography Revisited' (Eds J. B. Losos and R. E. Ricklefs.) pp. 13–51. (Princeton University Press: Princeton, NJ, USA.)

Louette, G., and De Meester, L. (2005). High dispersal capacity of cladoceran zooplankton in newly founded communities. *Ecology* **86**, 353–359. doi:10.1890/04-0403

Lucena-Moya, P., Pardo, I., and A´ lvarez, M. (2009). Development of a typology for transitional waters in the Mediterranean ecoregion: the case of the islands. *Estuarine, Coastal and Shelf Science* **82**, 61–72. doi:10.1016/J.ECSS.2008.12.011

MacArthur, R. H., and Wilson, E. O. (1967). 'The Theory of Island Biogeography', Vol. 1. (PrincetonUniversity Press: Princeton,NJ,USA.)

Magurran, A. E. (2013). 'Measuring Biological Diversty.' (John Wiley & Sons.)

Melendez-Hevia, I. (2004). 'Geología de España: una historia de seiscientos millones de años.' (Rueda.) Ministerio de Agricultura Pesca y Alimentación (2006). Sistema de identificación de parcelas agrícolas. Available at http://sigpac.mapa.es/fega/visor/ [Verified 20 December 2014].

Nielsen, D. L., Brock, M. A., Petrie, R., and Crossle´, K. (2007). The impact of salinity pulses on the emergence of plant and zooplankton from wetland see and egg banks. *Freshwater Biology* **52**, 784–795. doi:10.1111/J.1365-2427.2006.01714.X

Novosolov, M., and Meiri, S. (2013). The effect of island type on lizard reproductive traits. *Journal of Biogeography* **40**, 2385–2395. doi:10.1111/JBI.12179

Pérez-Ruzafa, A., Fernández, A. I., Marcos, C., Gilabert, J., Quispe, J. I., and Garcia-Charton, J. A. (2005). Spatial and temporal variations of hydrological conditions, nutrients and chlorophyll-*a* in a Mediterranean coastal lagoon (Mar Menor, Spain). *Hydrobiologia* **550**, 11–27. doi:10.1007/S10750-005-4356-2

Pérez-Ruzafa, A., Marcos, C., Pe´rez-Ruzafa, I. M., and Pérez-Marcos, M. (2011). Coastal lagoons: 'transitional ecosystems' between transitional and coastal waters. *Journal of Coastal Conservation* **15**, 369–392. doi:10.1007/S11852-010-0095-2

Pinheiro, J. C., and Bates, D. M. (2000). 'Mixed-effects Models in S and S-PLUS. Statistics and Computing.' (Springer. New York.)

Poff, N. L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**, 391–409. doi:10.2307/1468026

Quintana, X. D., Moreno-Amich, R., and Comın, F. A. (1998). Nutrient and plankton dynamics in a Mediterranean salt marsh dominated by incidents of flooding. Part 1: differential confinement of nutrients. *Journal of Plankton Research* **20**, 2089–2107. doi:10.1093/PLANKT/20.11.2089

Rossi, V., Benassi, G., Veneri, M., Bellavere, C., Menozzi, P., Moroni, A., and Mckenzie, K. G. (2003). Ostracoda of the Italian ricefields thirty years on: new synthesis and hypothesis. *Journal of Limnology* **62**, 1–8. doi:10.4081/JLIMNOL.2003.1

Sauer, J. D. (1969). Oceanic islands and biogeographical theory: a review. *Geographical Review* **59**, 582–593. doi:10.2307/213863

Shurin, J. B. (2000). Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* **81**, 3074–3086. doi:10.1890/0012-9658(2000)081[3074:DLIRAT]2.0.CO;2

Simon, C. (1987). Hawaiian evolutionary biology: an introduction. *Trends in Ecology & Evolution* **2**, 175–178. doi:10.1016/0169-5347(87)90015-2

Statzner, B., Hildrew, A. G., and Resh, V. H. (2001). Species traits and environmental constraints: entomological research and the history of ecological theory. *Annual Review of Entomology* **46**, 291–316. doi:10.1146/ANNUREV.ENTO.46.1.291

Strange, E. M., and Foin, T. C. (1999). Interaction of physical and biological processes in the assembly of stream fish communities. In 'Ecological Assembly Rules: Perspectives, Advances, Retreats'. (Eds E. Weiher and P. Keddy.) pp. 311–338. (Cambridge University Press: Cambridge, UK.)

ter Braak, C. J. F., and Sˇ milauer, P. (1998). 'CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4).' (Microcomputer Power: Ithaca, NY.)

Vanschoenwinkel, B., Gielen, S., Seaman, M., and Brendonck, L. (2008). Any way the wind blows: frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* **117**, 125–134. doi:10.1111/J.2007.0030-1299.16349.X

Venables, W. N., and Ripley, B. D. (2002). 'Statistics Complements to Modern Applied Statistics with S', 4th edn. (Springer: New York.)

Wallace, A. R. (1902). 'Island life', 3rd edn. (MacMillan and Co.: London)

Walter, H. S. (2004). The mismeasure of islands: implications for biogeographical theory and the conservation of nature. *Journal of Biogeography* **31**, 177–197. doi:10.1046/J.0305-0270.2003.00989.X

Watson, M. D. (2009). Continental Islands. In 'Encyclopedia of Islands'. (Eds R. G. Gillespie and D. A. Clague.) pp. 180–187. (University of California Press: Berkeley, CA.)

Whittaker, R. J., and Ferna´ndez-Palacios, J. M. (2007). 'Island Biogeography: Ecology, Evolution, an Conservation', 2nd edn. (Oxford University Press: Oxford.)

Whittaker, R. J., Triantis, K. A., and Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**, 977–994. doi:10.1111/J.1365-2699.2008.01892.X

Zamora, L., Mezquita, F., and Pretus, J. L. (2005). The non-marine ostracod fauna of the Balearic Islands. *Berliner pala¨obiologische Abhandlungen* **6**, 133.

**Table 1. Environmental variables from the studied coastal wetlands**

The mean ± s.d. are shown for each season and for each region of study. DIN, dissolved inorganic nitrogen

| Environmental variables | Archipelago | | Mainland | |
|---|---|---|---|---|
| | Winter | Spring | Winter | Spring |
| Size (ha) | 251 ± 240 | | 29 ± 16 | |
| Chlorophyll *a* (µg $L^{-1}$) | 5.60 ± 1.40 | 9.16 ± 1.94 | 9.64 ± 2.41 | 18.65 ± 3.28 |
| pH | 8.17 ± 0.09 | 8.22 ± 0.09 | 8.04 ± 0.11 | 8.05 ± 0.12 |
| Water temperature (°C) | 13.79 ± 0.88 | 24.34 ± 0.65 | 11.41 ± 0.41 | 25.29 ± 1.08 |
| Conductivity (mS $cm^{-1}$) | 7.41 ± 1.03 | 18.69 ± 3.06 | 11.19 ± 2.34 | 12.75 ± 2.63 |
| Dissolved oxygen (%) | 95.73 ± 4.42 | 73.23 ± 5.72 | 81.45 ± 4.44 | 91.66 ± 12.05 |
| Phosphate (µM) | 3.92 ± 0.56 | 1.93 ± 0.81 | 3.11 ± 1.67 | 4.37 ± 1.93 |
| DIN (µM) | 123.16 ± 32.48 | 30.58 ± 13.87 | 136.94 ± 42.75 | 148.67 ± 53.35 |

**Table 2. Descriptive parameters of the crustacean assemblage in the coastal wetlands from the Archipelago and the Mainland**

Occurrence is given as the percentage of samples in which the crustaceans were found

| | Cumulative species richness | | Common species (%) | | Occurrence (%) | |
|---|---|---|---|---|---|---|
| | Archipelago | Mainland | Archipelago | Mainland | Archipelago | Mainland |
| Cladocera | 13 | 18 | 53.80 | 38.90 | 40.60 | 62.50 |
| Ostracoda | 12 | 13 | 58.30 | 53.80 | 90.60 | 81.30 |
| Copepoda | 17 | 24 | 76.50 | 54.20 | 81.30 | 100.00 |
| Malacostraca | 16 | 12 | 31.30 | 41.70 | 93.80 | 62.50 |

**Table 3. Summary of similarity percentage analysis (SIMPER)**

The contribution to the average resemblances within sample groups (Contrib%) and the cumulative percentage (Cum.%) of characteristic species are given. The average dissimilarity between groups (Mainland *v*. Archipelago) was 85.29%. Asterisks indicate exclusive species (i.e. those that only appear in one region of the study). CLA, Cladocera; OST, Ostracoda; COP, Copepoda; MAL, Malacostraca.

| Species | Contrib% | Cum.% |
|---|---|---|
| Archipelago (average similarity: 24.25%) | | |
| *Cyprideis torosa* (OST) | 25.91 | 25.91 |
| *Gammarus aequicauda* (MAL) | 22.14 | 48.04 |
| *Lekanesphaera hookeri* (MAL) | 19.63 | 67.67 |
| *Loxoconcha elliptica* (OST) | 5.55 | 73.22 |
| *Heterocypris salina* (OST) | 3.36 | 76.58 |
| *Palaemonetes varians* (MAL) | 2.59 | 79.17 |
| *Simocephalus vetulus* (CLA) | 2.57 | 81.73 |
| *Sarscypridopsis aculeata* (OST) | 2.52 | 84.25 |
| *Calanipeda aquaedulcis* (COP) | 2.29 | 86.54 |
| *Daphnia magna*(CLA) | 1.66 | 88.2 |
| *Megacyclops viridis* (COP) | 1.39 | 89.59 |
| *Corophium acherusicum* (MAL) | 1.08 | 90.67 |
| Mainland (average similarity: 9.50%) | | |
| *Acanthocyclops* gr. *robustus* (COP) | 32.99 | 32.99 |
| *Gammarus aequicauda* (MAL) | 25.55 | 25.55 |
| *Chydorus sphaericus* (CLA) | 7.87 | 42.78 |
| *Calanipeda aquaedulcis* (COP) | 6.9 | 49.68 |
| *Diacyclops bicuspidatus* (COP)* | 5.84 | 55.52 |
| *Eucyclops serrulatus* (COP) | 4.79 | 60.31 |
| *Heterocypris salina* (OST) | 4.25 | 64.56 |
| *Lekanesphaera hookeri* (MAL) | 4.01 | 68.57 |
| *Macrocyclops albidus* (COP) | 3.05 | 71.62 |
| *Cyprideis torosa* (OST) | 2.75 | 74.37 |
| *Cypridopsis vidua* (OST)* | 2.48 | 76.85 |
| *Simocephalus vetulus* (CLA) | 2.27 | 79.12 |
| *Eucypris virens* (OST) | 2.18 | 81.3 |
| *Tropocyclops prasinus* (COP) | 1.97 | 83.27 |
| *Daphnia magna* (CLA) | 1.75 | 85.03 |
| *Daphnia pulicaria* (CLA)* | 1.6 | 86.62 |
| *Eurytemora velox* (COP)* | 1.35 | 87.98 |
| *Pleuroxus adundus* (CLA) | 1.28 | 89.25 |
| *Loxoconcha elliptica* (OST) | 1.27 | 90.53 |

**Table 4. Results from canonical correspondence analyses (CCAs): combined (Archipelago and Mainland) and for each region separately**

The order of the significant explanatory variables that had the best fit for species variability are indicated with numbers from 1 to 6. Variance explained by the first two axes is also shown. %λ, conditional effect expressed as percentage. DIN, dissolved inorganic nitrogen; Chl-*a*, chlorophyll *a*

| Explanatory variables | Combined CCA | | Archipelago CCA | | Mainland CCA | |
|---|---|---|---|---|---|---|
| | Best fit | %λ | Best fit | %λ | Best fit | %λ |
| Region | 1 | 24.66 | | | | |
| Conductivity | 2 | 19.73 | 1 | 24.58 | 1 | 20.08 |
| Temperature | 3 | 10.31 | 2 | 16.20 | | |
| Size | 4 | 9.42 | 4 | 11.17 | 2 | 16.47 |
| DIN | 5 | 8.52 | 3 | 13.97 | 3 | 15.26 |
| Chl-*a* | 6 | 8.07 | | | 4 | 14.06 |
| Phosphate | | | | | 5 | 11.24 |
| Variance explained (%) | | | | | | |
| Axis 1 | 4.3 | | 5.6 | | 5.0 | |
| Axis 2 | 7.1 | | 8.9 | | 9.7 | |

**Fig. 1.** Location of the coastal wetlands sampled (black dots) on the Catalonian mainland ('Mainland) and on the Balearic Islands ('Archipelago'): 1, Minorca; 2, Majorca; 3, Ibiza; 4, Formentera.

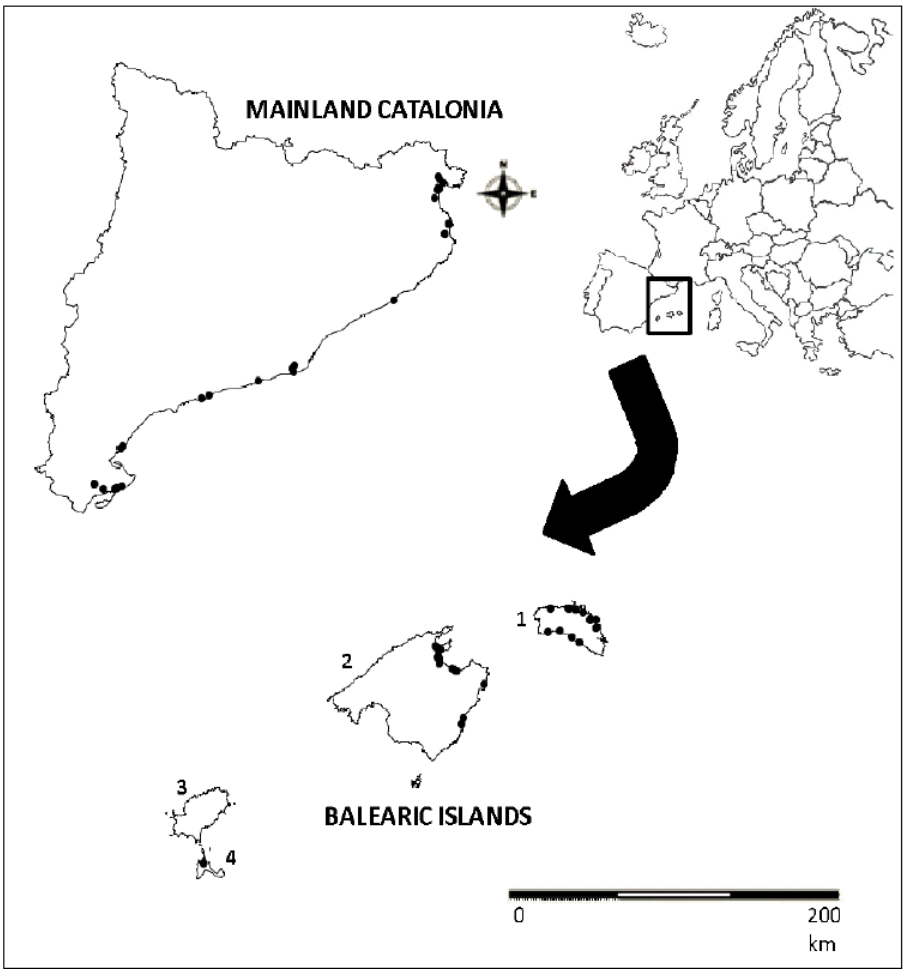


**Fig. 2.** Plot showing the centroids for the Mainland (MAIN) and the Archipelago (ARCH) regions in spring and winter taking into account all the environmental variables (see Table 1).

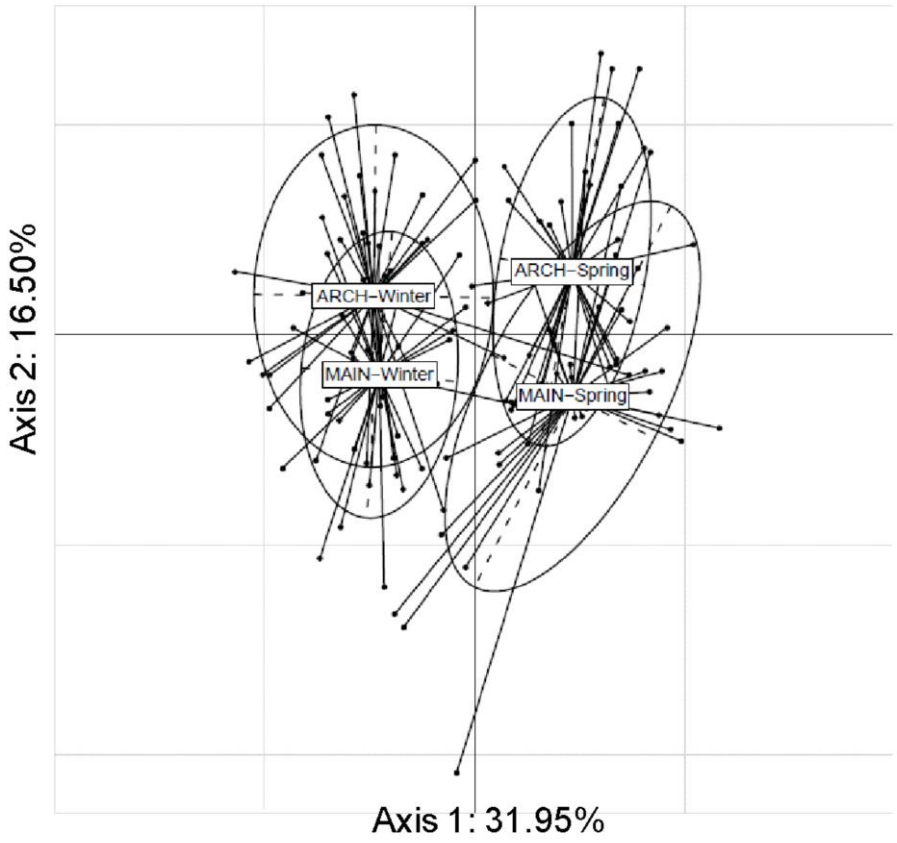


**Fig. 3.** Representation of the three diversity levels considered: (*a*) α diversity as mean species richness (mean ± s.d.), (*b*) β diversity as Simpson-based multiple-site dissimilarity ($\beta_{SIM}$) and nestedness-resultant multiple-site dissimilarity ($\beta_{NES}$) and (*c*) γ diversity as total species richness estimated using Chao2. Data are the mean ± 95% confidence intervals. *, $P < 0.01$; **, $P < 0.001$. CLA, Cladocera; OST, Ostracoda; COP, Copepoda; MAL, Malacostraca.

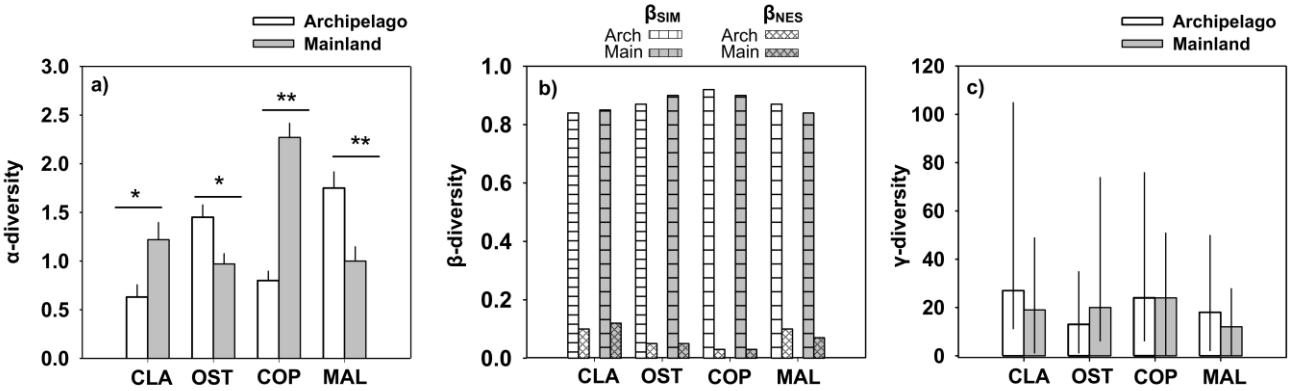
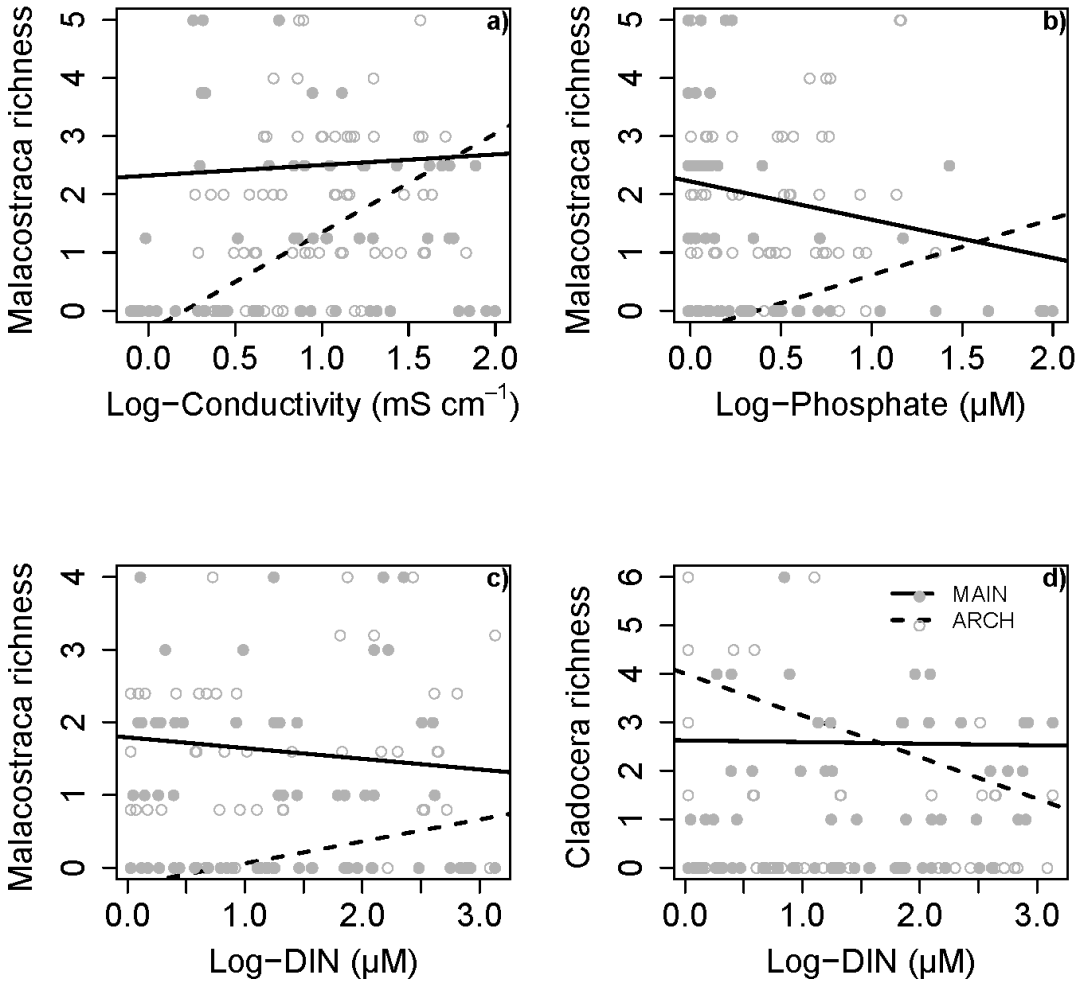



**Fig. 4.** Biplots showing the results of the linear mixed-effects models for those cases where a significant interaction with the regional factor (Archipelago (ARCH) or Mainland (MAIN)) was detected. DIN, dissolved inorganic nitrogen.



Supplementary material

**Table S1. List of crustaceans species identified in the Archipelago and Mainland**

+ indicates presence; – indicates absence. CLA, Cladocera; OST, Ostracoda; COP, Copepoda; CAL, Calanoida; CYC, Cyclopoida; HARP, Harpacticoida; MAL, Malacostraca; MYS, Mysidacea; AMPH, Amphipoda; ISO; Isopoda; TAN, Tanaidacea; DEC, Decapoda

| Species | Taxonomic Group | Archipelago | Mainland |
|---|---|---|---|
| *Alona guttata* Sars, 1862 | CLA | + | – |
| *Bosmina longirostris* (O.F. Müller, 1776) | CLA | – | + |
| *Camptocercus rectirostris* Schoedler, 1862 | CLA | – | + |
| *Ceriodaphnia laticaudata* P.E. Müller, 1867 | CLA | – | + |
| *Ceriodaphnia reticulata* (Jurine, 1820) | CLA | – | + |
| *Chydorus sphaericus* (O.F. Müller, 1785) | CLA | + | + |
| *Coronatella rectangula* (Sars, 1861) | CLA | + | + |
| *Daphnia curvirostris* Eylman, 1887 | CLA | + | – |
| *Daphnia magna* Straus, 1820 | CLA | + | + |
| *Daphnia pulicaria* Forbes, 1893 | CLA | + | + |
| *Leydigia acanthocercoides* (Fischer, 1854) | CLA | + | – |
| *Leydigia leydigii* (Schödler, 1862) | CLA | – | + |
| *Megafenestra aurita* (Fischer, 1849) | CLA | – | + |
| *Moina micrura* Kurz, 1874 | CLA | – | + |
| *Ovalona* cf. *anastasia* (Frenzel and Alonso 1988) | CLA | + | – |
| *Oxyurella tenuicaudis* (Sars, 1862) | CLA | – | + |
| *Pleuroxus aduncus* (Jurine, 1820) | CLA | + | + |
| *Pleuroxus denticulatus* Birge, 1879 | CLA | – | + |
| *Pleuroxus laevis* Sars, 182 | CLA | – | + |
| *Scapholeberis mucronata* (O.F. Müller, 1776) | CLA | – | + |
| *Scapholeberis rammneri* Dumont and Pensaert, 1983 | CLA | + | – |
| *Simocephalus exspinosus* (DeGeer, 1778) | CLA | + | + |
| *Simocephalus vetulus* (O.F. Müller, 1776) | CLA | + | + |
| *Tretocephala ambigua* (Lilljeborg, 1900) | CLA | + | – |
| *Bradleystrandesia reticulata* (Zaddach, 1844) | OST | – | + |
| *Candona angulata* G. W. Müller, 1900 | OST | + | – |
| *Candonocypris* sp. Sars, 1894 | OST | – | + |
| *Cyprideis torosa* (Jones, 1850) | OST | + | + |
| *Cypridopsis hartwigi* G. W. Müller | OST | + | – |
| *Cypridopsis vidua* (O. F. Müller, 1776) | OST | – | + |
| *Cypris bispinosa* Lucas, 1849 | OST | + | – |
| *Cypris subglobosa* Sowerby, 1840 | OST | – | + |
| *Eucypris virens* (Jurine, 1820) | OST | + | + |
| *Herpetocypris brevicaudata* Kaufmann, 1900 | OST | – | + |
| *Herpetocypris chevreuxi* (Sars, 1896) | OST | + | – |
| *Heterocypris incongruens* (Ramdohr, 1808) | OST | + | + |

| | | | |
|---|---|---|---|
| *Heterocypris salina* (Brady, 1868) | OST | + | + |
| *Ilyocypris getica* Masi, 1905 | OST | + | – |
| *Ilyocypris gibba* (Ramdohr, 1808) | OST | – | + |
| *Loxoconcha elliptica* Brady, 1868 | OST | + | + |
| *Plesiocypridopsis newtoni* (Brady & Robertson, 1870) | OST | + | + |
| *Sarscypridopsis aculeata* (Costa, 1847) | OST | + | + |
| *Arctodiaptomus salinus* (Daday 1885) | COP (CAL) | + | – |
| *Arctodiaptomus wierzejski* (Richard, 1888) | COP (CAL) | + | – |
| *Calanipeda aquaedulcis* Kritschagin, 1873 | COP (CAL) | + | + |
| *Eurytemora velox* (Lilljeborg, 1853) | COP (CAL) | – | + |
| *Mixodiaptomus kupelwieseri* (Brehm, 1907) | COP (CAL) | – | + |
| *Acanthocyclops* gr. *robustus* (Sars, 1863) | COP (CYC) | + | + |
| *Cyclops* sp.O. F. Müller, 1776 | COP (CYC) | – | + |
| *Diacyclops bicuspidatus* (Claus, 1857) | COP (CYC) | – | + |
| *Diacyclops bisetosus* (Rehberg, 1880) | COP (CYC) | – | + |
| *Ectocyclops phaleratus* (Koch, 1838) | COP (CYC) | – | + |
| *Eucyclops macruroides* (Lilljeborg, 1901) | COP (CYC) | – | + |
| *Eucyclops serrulatus* (Fischer, 1851) | COP (CYC) | + | + |
| *Halicyclops rotundipes* Kiefer, 1935 | COP (CYC) | + | + |
| *Macrocyclops albidus* (Jurine, 1820) | COP (CYC) | + | + |
| *Megacyclops viridis* (Jurine, 1820) | COP (CYC) | + | + |
| *Microcyclops rubellus* (Lilljeborg, 1901) | COP (CYC) | + | + |
| *Paracyclops fimbriatus* (Fischer, 1853) | COP (CYC) | – | + |
| *Thermocyclops dybowskii* (Landé, 1890) | COP (CYC) | + | + |
| *Tropocyclops prasinus* (Fischer, 1860) | COP (CYC) | + | + |
| *Canthocamptus staphylinus* (Jurine, 1820) | COP (HAR) | + | + |
| *Canuella perplexa* T. and A. Scott, 1893 | COP (HAR) | + | + |
| *Cletocamptus confluens* (Schmeil, 1894) | COP (HAR) | + | + |
| *Cletocamptus retrogressus* Schmankevitsch, 1875 | COP (HAR) | + | – |
| *Eudactylopus* sp. cf. Scott, 1909 | COP (HAR) | + | – |
| *Harpacticus littoralis* Sars, 1910 | COP (HAR) | – | + |
| *Nitocra lacustris* (Shmankevich, 1875) | COP (HAR) | – | + |
| *Schizopera* sp. (cf. *compacta)* Lint, 1922 | COP (HAR) | – | + |
| *Tisbe longicornis* (T. and A. Scott,, 1895) | COP (HAR) | + | + |
| *Atyaephyra desmarestii* (Millet, 1831) | MAL (DEC) | – | + |
| *Corophium acherusicum* Costa, 1857 | MAL (AMP) | + | – |
| *Corophium insidiosum* Crawford, 1937 | MAL (AMP) | + | – |
| *Corophium orientale* Schellenberg, 1928 | MAL (AMP) | + | + |
| *Corophium sextonae* Hurley, 1954 | MAL (AMP) | + | – |
| *Cyathura carinata* (Kroyer, 1847) | MAL (ISO) | + | – |
| *Echinogammarus pacaudi* (Hubault and Ruffo, 1956) | MAL (AMP) | – | + |
| *Echinogammarus stocki* Karaman, 1969 | MAL (AMP) | + | – |
| *Gammarus aequicauda* (Martyinov, 1931) | MAL (AMP) | + | + |
| *Gammarus insensibilis* Stock, 1966 | MAL (AMP) | + | – |

| | | | |
|---|---|---|---|
| *Heterotanais oerstedi* (Kroyer, 1842) | MAL (TAN) | – | + |
| *Lekanesphaera hookeri* (Leach, 1814) | MAL (ISO) | + | + |
| *Leptocheirus pilosus* Zaddach, 1844 | MAL (AMP) | – | + |
| *Mesopodopsis slabberi* (Van Beneden, 1861) | MAL (MYS) | – | + |
| *Microdeutopus* sp.Costa, 1853 | MAL (AMP) | + | – |
| *Orchestia gammarellus* (Pallas, 1766) | MAL (AMP) | + | – |
| *Orchestia platensis* Hayat, 1998 | MAL (AMP) | + | – |
| *Palaemon elegans* Rathke, 1837 | MAL (DEC) | + | – |
| *Palaemon longirostris* Milne-Edwards, 1837 | MAL (DEC) | – | + |
| *Palaemonetes varians* (Leach, 1814) | MAL (DEC) | + | – |
| *Palaemonetes zariquieyi* Sollaud, 1939 | MAL (DEC) | – | + |
| *Proasellus coxalis* (Dollfus, 1892) | MAL (ISO) | + | + |
| *Procambarus clarkii* (Girard, 1852) | MAL (DEC) | + | + |
| Total species | 93 | 58 | 67 |
| Exclusive species | | 26 | 35 |

**Table S2. Summary of the LME results for the variable species richness**

The significance between regions was assessed using the conditional *F*-test of the intercept values (see Table S3), while the slopes inform about the relationship between the dependent variable (species richness) and the independent variables (continuous environmental parameters). Slope values of independent variables retained in each mixed effects model are shown for each region; when non-significant differences were detected for the slopes of each region (i.e., the same slope for both regions) then 'overall slope' is shown. The *t*-test obtained from each mixed effects model, indicating the significance of the slopes, is shown. The regional effect ('Region', i.e. Archipelago *v.* Mainland) is highlighted in bold. Cond, conductivity; Pho, phosphate; DIN, dissolved inorganic nitrogen; Chl-*a*, chlorophyll-*a*

| | | Slopes | | | | |
|---|---|---|---|---|---|---|
| Species richness | Variable | Archipelago | Mainland | Overall | *t*-Student | *P*-value |
| | Phosphate | | | 0.74 | 3.24 | 0.002 |
| Cladocera | Conductivity | | | –1.81 | –7.93 | 0.000 |
| d.f. = 121 | Region × DIN | –0.66 | –0.03 | | 3.31 | 0.001 |
| Ostracoda | Size | | | 0.29 | 4.12 | 0.000 |
| d.f. = 123 | Chl-*a* | | | 0.41 | 2.17 | 0.032 |
| | Region | | | | | |
| Copepoda | Conductivity | | | –0.58 | –2.75 | 0.007 |
| d.f. = 123 | Temperature | | | –1.18 | –2.27 | 0.025 |
| | Region | | | | | |
| | Chl-*a* | | | –0.59 | –2.15 | 0.034 |
| Malacostraca | Region × DIN | 0.43 | –0.15 | | –2.18 | 0.032 |
| d.f. = 118 | Region × Pho | 0.97 | –0.63 | | –2.56 | 0.012 |
| | Region × Cond | 1.70 | 0.20 | | –2.51 | 0.014 |

**Table S3. Complementary table to Table S2, where intercept values are shown**

*P*-values < 0.05 show significant differences in the intercept values of Mainland and Archipelago, i.e. significant differences of species richness between both regions

| Species richness | Intercept | | | | | |
|---|---|---|---|---|---|---|
| | Archipelago | Mainland | *F* | d.f.1 | d.f.2 | *P*-value |
| Cladocera | 2.75 | 2.63 | 0.19 | 1 | 121 | 0.667 |
| Ostracoda | –0.03 | –0.48 | 6.8 | 1 | 123 | 0.010 |
| Copepoda | 2.86 | 4.25 | 62.51 | 1 | 123 | <0.0001 |
| Malacostraca | –0.36 | 1.79 | 6.5 | 1 | 118 | 0.012 |